In vitro study of the biochemical origin and production limits of odorous compounds in cattle feedlots[1,2]

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ABSTRACT: Livestock odors are closely correlated to airborne concentrations of volatile organic compounds (VOC), which are a complex mixture of carbon-, sulfur-, and nitrogen-containing compounds produced primarily during the incomplete anaerobic fermentation of animal manure by microorganisms. Volatile fatty acids, alcohols, and aromatic ring compounds comprise a substantial fraction of VOC, yet very little is known about their biochemical origin and environmental factors controlling their production. The anaerobic production of fermentation products and consumption of substrates (CP, starch, and nonstarch carbohydrate) were analyzed in slurries of fresh (< 24 h) and aged (> 1 d) cattle manure over several weeks. Ethanol, acetate, propionate, butyrate, lactate, and H_2 were the major products of fermentation. Aged cattle manure produced twice the concentration of VFA during incubation produced by the fresh manure ($P < 0.001$). Aromatic compounds (phenols, indoles, and benzoates) remained unchanged in both manures. Production of VFA from fresh manure was inhibited when the pH fell below 4.5. It is likely that the presence of calcareous soil, which has a high buffering capacity, and lactate-consuming microorganisms minimized acidification in the aged manure slurries. Low starch content limited VFA production in the aged manure. Starch was the likely biochemical source for fermentation products in both manures based on the strong negative correlations between fermentation product and starch content (r = –0.944 and –0.773) and ratio of fermentation products produced to starch consumed (r = 0.64 and 0.72) for fresh and aged manure, respectively. Nonstarch carbohydrate served an indeterminate role in the production of fermentation products. Nonstarch carbohydrate decreased by 4.7 and 23.4 g/L in the fresh and aged manure, respectively, whereas the starch content decreased by 18.6 and 22.4 g/L in the fresh and aged manure, respectively. The concentration of CP did not change, which suggests a balance between protein consumption and new bacterial biomass production. We conclude that the types of substrates in cattle manure and the feedlot soils where they are deposited are significant factors in the production of odors.

Key Words: Bacteria, Cattle, Manures, Odors

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Introduction

Agricultural odors present an increasingly difficult challenge to livestock producers, yet very little information is available on the microbiology of odor production and factors limiting their emission. Livestock odors are produced primarily during the incomplete anaerobic fermentation of livestock waste by bacteria (Mackie et al., 1998). This complex chemical mixture includes VFA, alcohols, aromatic compounds, amides (including NH_3), and sulfides (O'Neill and Phillips, 1992; Hartung and Phillips, 1994). Concentrations of airborne VFA and volatile aromatic compounds most closely correlate to odor (Zahn et al., 1997; Zhu et al., 1997; Zahn et al., 2001a). Limiting the production of these compounds during manure decomposition should decrease odor emissions. Both carbohydrates and proteins are biochemical precursors to these compounds (Mackie et al., 1998; Zhu et al., 1999), but there is no clear consensus on their relative contributions to malodor.

We hypothesized that 1) malodorous VFA are the dominant cattle manure fermentation products produced almost exclusively by carbohydrate fermentation; 2) the production of branched-chain VFA and aromatic compounds is minimal, arising from a limited protein fermentation; and 3) the accumulation of acid

[1]Names are necessary to report factually on available data; however, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by USDA implies no approval of the product to the exclusion of others that may also be suitable.

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products is self-limiting, as low pH inhibits fermentation. In this study, the composition of fresh and aged cattle manure and the accumulation of fermentation products were monitored in anaerobic slurries for 5 wk in order to determine factors limiting odor compound accumulation and to identify their biochemical precursors (starch, nonstarch carbohydrate, or protein). The scope of this study was restricted to monitoring only odor compounds in the liquid phase of the manure slurry, the ultimate source of airborne odors at cattle feedlots. Other factors that influence airborne odor concentrations, such as temperature, precipitation, air speed, and humidity, are beyond the scope of this study.

Materials and Methods

Feedlot Description

Soil samples were collected at the 6,000-animal capacity, open-air cattle feedlot at the USDA, U.S. Meat Animal Research Center located in south-central Nebraska. Two types of feedlot samples, fresh and aged manures, were collected from six adjacent feedlot pens during September 2000. Each pen held 30 steers born in the fall of 1999. The fresh samples were < 24 h old manure (i.e., had not formed a crust), and the aged samples were of unconsolidated surface material consisting of dried cattle manure and loose soil. Cattle were fed 9.7 kg DM/steer daily of a diet that contained 83% corn, 13% corn silage, and 4% liquid supplement on a DM basis. The supplement was 75% CP and included a nonprotein nitrogen content of 71% (of the CP), 11% Ca, 1% P, 70,000 IU vitamin A/kg, 152 IU vitamin E/kg, and 0.306 g monensin/kg (Elanco Animal Health, Greenfield, IN).

Odor Production Experiments

For odor production experiments, 1 kg of manure (fresh or aged) was blended by Waring blender (New Hartford, CT) with a mixture of 700 mL of HCl-preserved (20 m*M* final concentration) cattle urine, 2.8 g urea, and 3.3 L of 12.12 m*M* H_2KPO_4 (pH 7.5). The urea and phosphate buffer were added to the urine to replenish urea hydrolyzed during storage and to neutralize the acid used for preservation. Roughly 180 mL of the manure slurry was then added to five 250-mL flasks, gassed with N_2, stoppered, and incubated at room temperature (20 to 23°C). Excess fermentation gas was vented though a needle into a water-filled test tube. At periods ranging from daily to weekly, gas and slurry samples were collected. Dry matter content and OM content of the composites were measured by weight differences upon drying at 100°C overnight and after combusting the sample overnight at 560°C, respectively. Slurry pH was measured using a combination pH electrode and PHM 80 Portable pH meter (Radiometer Analytical, Westlake, OH). Headspace gases (O_2, H_2, and CH_4) were monitored during the incubation using a Varian 3300 gas chromatograph (Walnut Creek, CA) equipped with a thermal conductivity detector (200°C). Typically, 0.5 mL of headspace gas was injected directly onto a Mol Sieve 5A, 80/100 mesh column (3.05 m × 3 mm, oven temp = 70°C, flow rate 20 mL N_2/min). The identities and concentrations of headspace gases were determined by comparison to the retention times and responses of known standards.

A portion of each manure slurry sample was centrifuged and the supernatant was analyzed for L-lactate and fermentation products (VFA, alcohols, and aromatics, see below). L-lactate was determined using a membrane-immobilized enzyme system (YSI Model 27, Yellow Springs Instrument Co., Yellow Springs, OH). Another portion (4 mL) was immediately analyzed for pH (see above), preserved by the addition of 0.2 mL of 1 *M* NaOH, and frozen for substrate content (protein, total carbohydrate, and starch) analyses. A third 2-mL portion of slurry was combined with 2 mL of 2 *M* KCl and shaken for 1 h. The supernate was clarified by centrifugation at 10,000 × *g* and preserved by the addition of 20 μL of concentrated H_2SO_4. Ammonia and urea were determined in the KCl extracts using a Technicon auto-analyzer (Technicon, Tarrytown, NY) as previously described (Varel et al., 1999). Urea and ammonia nitrogen were determined by a modification of the carbamido-diacetyl reaction and indophenol blue methods, respectively. After sampling, the headspace of each flask was gassed with N_2 to remove any oxygen.

Samples for biochemical analysis were thawed, homogenized two times for 15 s using an OMNI 5000 homogenizer (OMNI International, Warrenton, VA), and diluted with H_2O. Total carbohydrate was determined colorimetrically using the phenol-sulfuric acid reaction (Daniels et al., 1994) after an initial acid hydrolysis (2.5% phenol and 30% H_2SO_4 final concentration). Starch was determined as free glucose using the YSI analyzer (see above) after autoclaving the sample for 1 h and digesting overnight with amyloglucosidase at 55°C (MacRae and Armstrong, 1968). Nonstarch carbohydrate was calculated as the difference between total carbohydrate and starch. For CP content, samples were made alkaline (1 *M* NaOH, final concentration) and dried overnight at 100°C to remove free NH_3. Crude protein content was then determined using a LECO CN-2000 carbon/nitrogen analyzer (LECO, St. Joseph, MI).

Odor Compound and Statistical Analyses

Odorous compounds (alcohols, VFA, and aromatic compounds) were quantified only in the liquid phase of the slurries. No measurements were made of the gas-phase constituents. On the day of analysis, 1-mL frozen slurry samples were centrifuged at 10,000 × *g* for 5 min. A 0.5-mL portion of the supernate was combined with an internal standard (ethyl butyrate; 0.25 m*M* final concentration) in an autosampler vial, acidified by the addition of 40 μL of 3 *M* HCl, and capped. Odorous compounds in each vial were analyzed relative to standards containing known concentrations of odorous compounds using a Hewlett Packard 6890 gas chromatograph (Agilent Technologies, Palo Alto, CA) equipped with a flame ionization detector and a Hewlett Packard 5973 mass selective detector (Agilent Technologies, Palo Alto, CA). Compounds were separated on a 30 m × 0.32 mm diameter (0.5 μm film thickness) Innowax PEG column (Agilent Technologies) using the following program parameters: initial flow rate = 0.5 mL/min for 1 min, ramp flow of 5 mL/min to 10 mL/min, initial temp = 70°C, initial time = 4 min, first temp ramp = 12°C/min to 160°C, second temp ramp = 6°C/min to 181°C, hold at 181°C for 1 min, final temp ramp = 4°C/min to 211°C. Injector temperature was 275°C and detector temperature was 250°C. The concentrations and identities of sample odorous compounds were determined by flame ionization and by comparison to the retention times and responses of known standards. The identities of odorous compounds were confirmed in selected samples by mass spectroscopy (EM voltage = 1,700; MS Quad = 150°C; MS Source = 230°C; National Institute of Standards and Technology 1998 reference library, Washington, DC).

Data were analyzed as a split plot in time. The unit of observation in this study was the flask. The model included age of manure, day, flask (manure), and the manure × day interaction with manure and day as main effects. Manure was tested with flask (manure) as the source of error. Differences between least squares means were tested with a protected *t*-test. For discussion, responses with $P < 0.05$ were considered to differ. Statistical analyses were done with the GLM procedure of SAS (version 7.0; SAS Inst. Inc., Cary, NC).

Results and Discussion

Accumulation of Odorous Compounds and Fermentation Products in Manure Slurries

The accumulation of odorous compounds and fermentation products differed between fresh manure and aged samples but was dominated by VFA and alcohol production (Figure 1A to F), which was consistent with our first hypothesis (VFA are the primary fermentation products of cattle manure). Ethanol was produced at high concentrations (25 to 40 m*M*) in both slurries, comprising > 95% of the total alcohol accumulated during the first 2 wk of manure fermentation (Figure 1A, B). At d 10, when alcohol concentrations were highest, propanol and butanol were the next most abundant alcohols in the manure slurries and comprised roughly 3% and 1%, respectively, of the total alcohol. A notable difference in alcohol accumulation between the manures was the consumption of ethanol at the end of incubation in the aged manure slurries.

Initial rates of total VFA accumulation were very similar for both the fresh and the dry manures (Figure 1C, D). However, total VFA concentration by d 15 from the aged manure was double that from the fresh manure because the accumulation of total VFA in the fresh manure stopped after d 4. Acetate, propionate, and butyrate comprised more than 98% of the total VFA in both manure slurries, but there were differences over time and between manures in the relative contributions of these VFA in the total VFA pool. For instance, butyrate comprised twice the total VFA in the aged manure during the 2nd wk of the incubation compared to the fresh manure ($P < 0.001$).

A diverse group of microorganisms produce alcohols, straight-chain VFA, and lactate as fermentation end-products through homofermentative, heterofermentative, and mixed acid fermentations (Moat, 1979). Recent studies have detected *Clostridium*, *Lactobacillus*, and *Bacillus* species in animal manures (T. Whitehead and M. Cotta, personal communication). Various microorganisms in these groups utilize these alcohol- and VFA-producing pathways, and it is likely that changes in their abundances and(or) activities are responsible for the patterns of alcohol, VFA, and lactic acid accumulation and consumption observed in this study. Lactic acid seems to be converted to butyrate at different times during fermentation for the fresh and aged manure slurries (Figure 1C, D). For the fresh manure, butyrate concentrations increased markedly after d 10, simultaneously with a loss of lactate and acetate. In the aged manure, there was an initial 2-d lag in butyrate accumulation, and then butyrate rapidly accumulated with a simultaneous decrease in lactate concentration. *Megasphaera elsdenii* and *Selenomonas ruminantium* are capable of transforming lactate to butyrate and have been used to combat lactic acidosis in ruminants (Kung and Hession, 1995). The activities of these or similar microorganisms in the fresh and aged manure may account for the dynamic changes in butyrate concentrations.

Production of branched-chain VFA and aromatic compounds has been linked to protein fermentation (Mackie et al., 1998). The production of branched-chain VFA (isobutyrate, isovalerate, and isohexanoate) was observed only after d 4 in the aged manure slurries and represented 4% (molar basis) of the total VFA (Figure 1C to D). Fresh manure slurries produced no branched-chain VFA. At the end of incubation, isobutyrate, isovalerate, and isohexanoate comprised 72, 25, and 3% of the total branched-chain VFA in the liquid phase of the aged manure slurries.

The concentrations of aromatic compounds (phenols, indoles, and benzoates) differed initially and showed a different pattern of production between the two manures (Figure 1E, F). The initial concentration of phenols (phenol, ρ-cresol, 4-ethyl phenol), indoles (indole and skatole), and benzoates (benzoate, phenyl acetate, phenyl propionate) were higher in the aged manure ($P < 0.001$). Phenol and cresol constituted a majority of the phenols (23 and 63%, respectively) in the fresh manure, whereas cresol and 4-ethyl phenol made up 40 and 45%, respectively, of the phenols in the aged manure slurries at the end of incubation. Phenol and 4-ethyl phenol

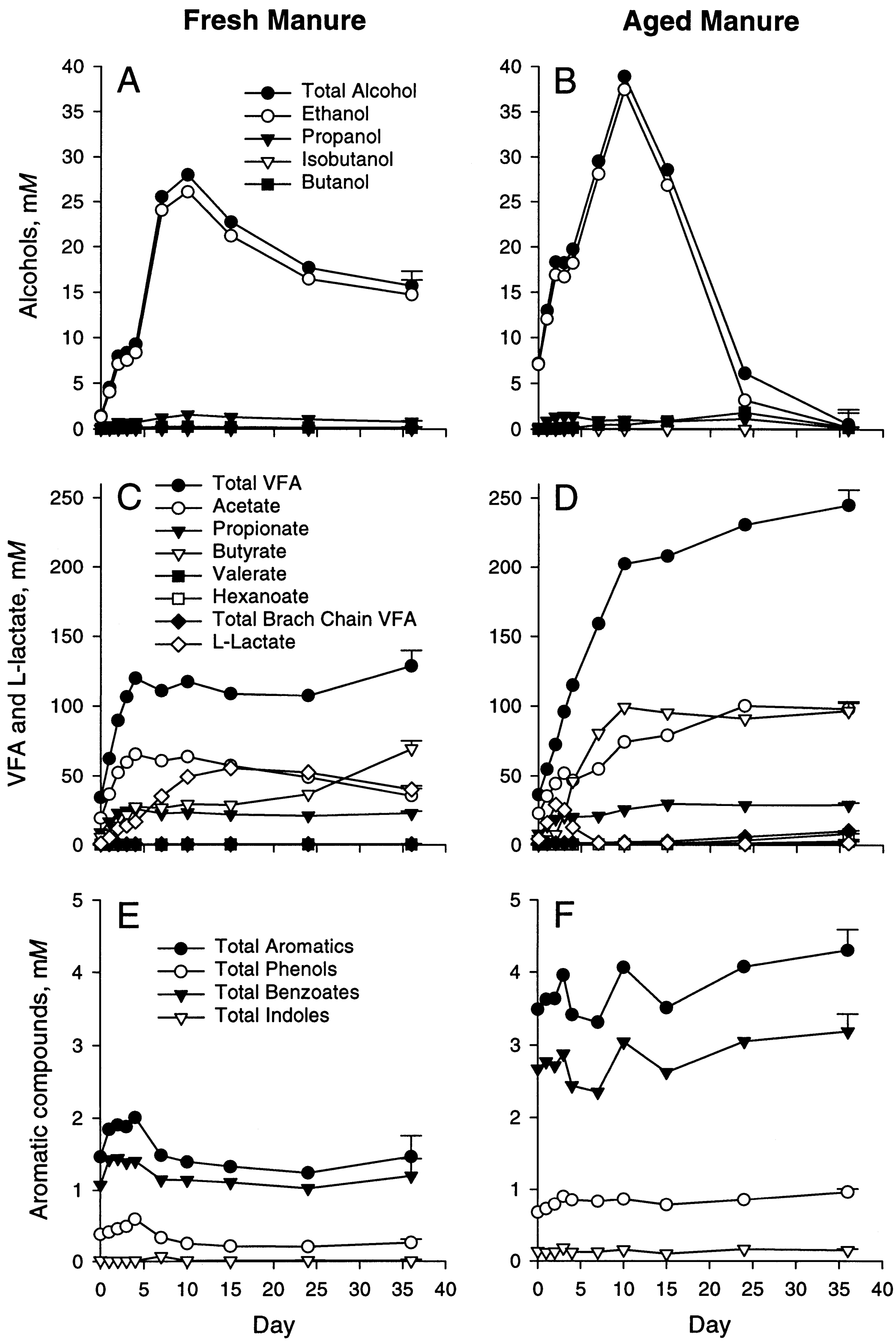

Figure 1. Concentrations of alcohols, acids, and aromatic compounds during incubation of fresh and aged cattle manure slurries. The SE of the least squares means (n = 5) for each compound is reported on d 36. All response variables for manure × day differed at $P < 0.001$ except for total aromatics ($P = 0.183$), total indoles ($P = 0.552$), and total benzoates ($P = 0.422$).

made up the balance, 15 and 14%, in aged and fresh manure slurries, respectively. In both manure slurries, there was no accumulation of aromatic compounds.

Some protein fermentation may have occurred even if there was no observed change in aromatic compound content or accumulation of branched-chain VFA. Fermentative bacteria could have utilized most of these fermentation products for protein and lipid biosynthesis (Moat, 1979). A comparison of our results to other studies (Macfarlane et al., 1992; Smith and Macfarlane, 1998), however, indicates that protein fermentation was very limited. Those studies of mixed-culture microbial fermentations that rely on protein for energy production and cell biosynthesis found a larger percentage of branched-chain VFA (16 to 21%) relative to total VFA and substantial increases in aromatic compounds. The low concentrations of branched-chain VFA and aromatic compounds in our cattle manure slurries indicate that protein fermentation was not a dominant process and supports our second hypothesis (limited protein fermentation).

Controls on Odor Compound Accumulation and Their Biochemical Origins

Substrate availability and the accumulation of acid end-products may have limited VFA production in the manure slurries. Lactate and VFA accumulation in the fresh manure slurries decreased the pH and probably affected fermentation and the production of CH_4 and H_2 gases (Figure 2A, B). In agreement with other studies (Switzenbaum et al., 1990), we observed that methanogenesis was inhibited below pH 6. In this and other unpublished studies from our laboratories, we observed that VFA production in cattle manure was also inhibited below pH 4.5. After d 3, methanogenesis was essentially inhibited, and when the pH of fresh manure slurries dropped below pH 4.5 (d 4 to 7), VFA production stopped (Figure 2C). These observations of the fresh manure slurries are consistent with our third hypothesis (acid limitation of VFA production), but acid limitation was not observed in the aged manure. In the aged manure slurries, the pH only decreased to 5.5, and VFA accumulated through d 24. Two possible mechanisms account for continued VFA production in aged manure slurries. First, the feedlot pen soil was calcareous and possessed considerable buffering capacity that minimized the effect of acid production. Second, lactic acid, which is a much stronger acid than standard VFA (Owens et al., 1998), accumulated only during the 1st wk of incubation in the aged manure slurries and at much lower concentrations compared to the fresh manure slurries (Figure 2A). It is likely that a population of soil microorganisms, capable of converting lactic acid into other VFA, converted the lactic acid into butyrate and minimized the pH decrease during fermentation. A future area of investigation is to examine why these bacteria are so active in aged vs fresh manure.

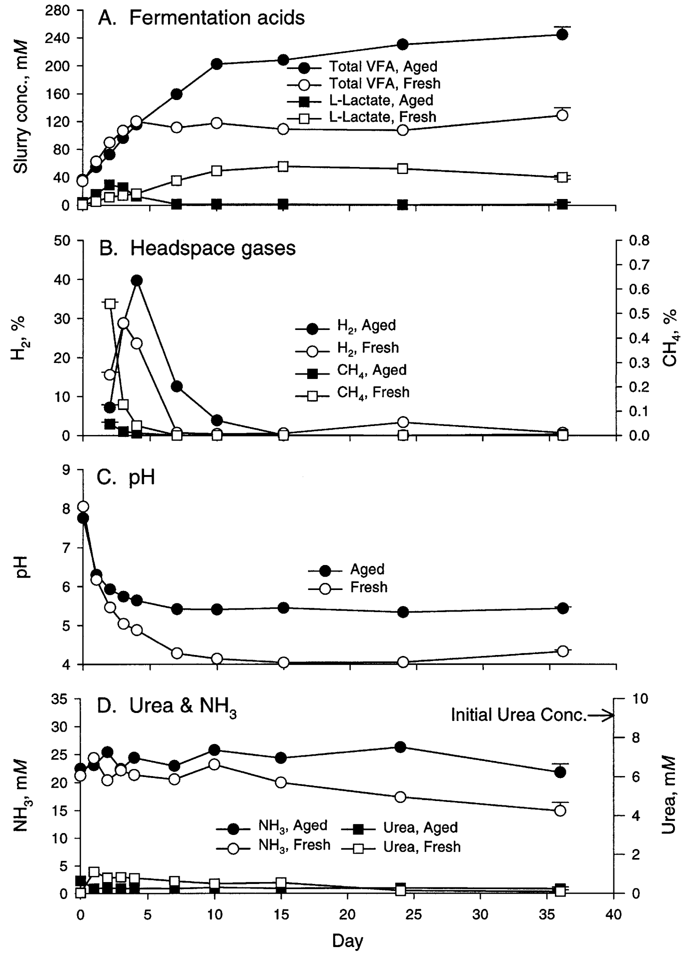

Figure 2. Production of total volatile fatty acid (VFA) and fermentation gases (H_2 and CH_4) in fresh and aged manure slurries in relation to pH, L-lactate, NH_3, and urea content. The SE of the least squares means (n = 5, n = 3 for headspace gases) for each compound is reported on d 36 (d 2 for headspace gases). All response variables for manure × day differed at $P < 0.001$ except for NH_3 ($P = 0.055$).

Ammonia in very high concentrations could act to buffer fermentations in the manure slurries. A large difference in NH_3 content of aged and fresh manures could also account for the higher pH in the aged manure slurries. However, both manure slurries had high, stable NH_3 concentrations throughout the course of incubation (Figure 2D), which argues against the likelihood of one manure being more NH_3-buffered than the other. Urea was the likely source of the NH_3, accounting for > 80% of the measured NH_3. The urea was added at roughly 9.3 m*M*, but it was rapidly hydrolyzed while the manures were mixed before initial sampling.

The concentrations of potential substrates, including CP, starch, and nonstarch carbohydrate, were analyzed in the manure slurries in order to identify the sources of malodorous VFA and to determine whether substrate availability limited VFA production in the aged manure slurries. In both fresh and aged manure slurries, starch

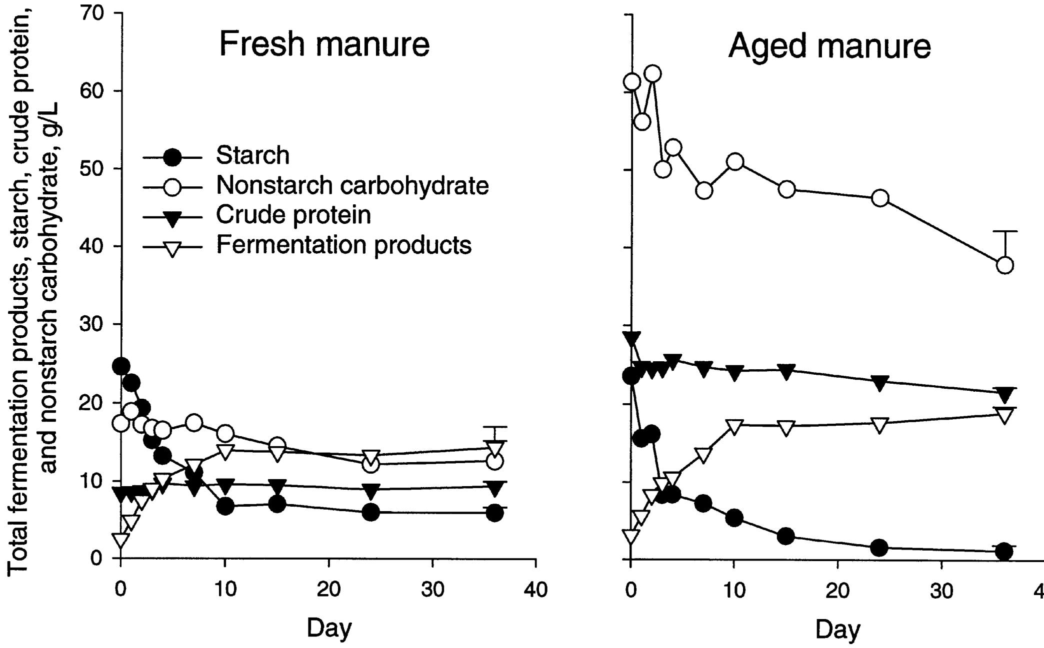

Figure 3. Relationships between the sum of total fermentation product concentration (alcohols + VFA + L-lactate) and protein, starch, and nonstarch carbohydrate content in the aged and fresh manure slurries during incubation. The SE of the least squares means (n = 5) for each compound is reported on d 36. All response variables for manure × day differed at $P < 0.001$ except for fermentation products ($P = 0.077$) and nonstarch carbohydrate ($P = 0.516$).

losses were associated with an increase in fermentation products (Figure 3). There were no significant changes in CP or nonstarch carbohydrate content in the fresh manure during incubation ($P > 0.2$), whereas there was a decrease in both CP (7 g/L) and nonstarch carbohydrate (23 g/L) in the aged waste by the end of the incubation ($P < 0.01$). Starch losses in the fresh manure slurries comprised 80% of the total carbohydrate loss, whereas starch losses in the aged manure slurries comprised 49% of the total carbohydrate loss. Total carbohydrate losses of 46 and 23 g/L were within the limits of OM losses (77 and 23 g/L) for aged and fresh manure slurries, respectively.

When the accumulation of fermentation products was examined in relation to cumulative substrate loss, a very strong correlation was observed between fermentation products produced and starch consumed in the fresh (r = 0.964, $P < 0.001$) and aged manure (r = 0.761, $P < 0.001$) slurries. Starch availability in the aged manure slurries seemed to limit the accumulation of fermentation products; as starch became depleted, no more fermentation products were produced (Figure 3). In the fresh manure slurries, the correlations between fermentation product accumulation and nonstarch carbohydrate or CP consumption were lower (r = 0.328 and –0.202, respectively). In the aged manure slurries, nonstarch carbohydrate consumption had a lower correlation with fermentation product accumulation (r = 0.151) than the correlation between fermentation product accumulation and CP consumption (r = 0.576). Starch, if it was the sole substrate, was converted into fermentation products at similar ($P > 0.5$) percentages of 64 and 72% (wt/wt) for fresh and aged manure, respectively, which is consistent with values measured in pure culture microbial studies of fermentative metabolism (Moat, 1979).

Based on these data, we conclude that starch fermentation was the chief biochemical source of the malodorous, liquid-phase VFA produced and that CP and nonstarch carbohydrate fermentation played a negligible role in fresh manures. For aged manures, carbohydrate was also a primary biochemical source; starch conversion to fermentation products was as important as all other carbohydrate sources combined. This finding is consistent with fermentation studies of human colonic bacteria in which increasing available carbohydrate decreased amino acid fermentation (Smith and Macfarlane, 1996; Smith and Macfarlane, 1998). During the course of the aged cattle manure incubation, easily fermentable starch was consumed preferentially over protein and nonstarch carbohydrate, and VFA was produced. The production of VFA in the aged manure slurries ended only after all available starch was consumed; thus, starch was probably the limiting factor for VFA production in this manure. Crude protein concentrations were unchanged during the incubations, reflecting a balance between true protein degradation and synthesis.

Further evidence for the importance of starch fermentation as the primary source of VFA was the initial composition of the fresh and aged manures. A comparison of aged and fresh manures on d 0 indicated that the aged manure contained less starch and tended to contain more CP before sampling (Figure 3). Initial starch concentrations in the aged manure made up a lower ($P < 0.001$) percentage (12.8%) of the OM than in the fresh manure (32.5%), whereas CP content tended ($P = 0.051$) to be a higher percentage (15.3 and 11.3% for aged and fresh manure, respectively) of the OM. No difference ($P > 0.1$) was measured between manures for nonstarch carbohydrate (33.7 and 22.9% for aged and fresh manure, respectively) and the total substrate (total carbohydrate + CP) pool (61.8 and 66.7% for aged and fresh manure, respectively). These observations are consistent with a model of initial starch fermentation in fresh manure as it dries out and mixes with soil on the feedlot surface. Over time, true protein content increases slightly as the fermenting microorganism biomass increases.

Odor Compound Production in the Feedlot

A variety of environmental factors including temperature, moisture, soil pH, humidity, and wind speed are critical factors influencing the emission and transport of odorous compounds away from concentrated animal production facilities (Zahn et al., 1997; 2001b). However, a prerequisite for large odor emissions is a preexisting large pool of odorous compounds in the feedlot soil. Temperature, soil moisture, and manure composition are probably the three primary factors controlling the onset, rate, and extent of anaerobic manure decomposition in cattle feedlot soils that supplies the pool of odorous compounds.

Based on the findings of this study, we propose the following conceptual model for the formation of soil-associated odor compounds. In typical dry feedlots, most of the feedlot surface is covered by aged manure mixed with soil. Freshly deposited manure will undergo initial starch fermentation, but the fermentation in the fresh manure will come to a stop as the pH drops below 4.5 (the VFA fermentation threshold) and(or) as the fresh manure dries out and mixes with feedlot soil. As a source of odor, the fresh manure would be a constant, but minor, source compared to the major odor emissions from aged manure, which covers the entire pen surface, after a rainfall. Earlier research has documented a 60-fold increase in odor concentrations after rainfall (Watts and Tucker, 1993; Watts et al., 1994). These researchers also observed significantly higher odor concentrations for cattle manures from animals fed diets with higher starch content. We propose that after a rainfall occurs, the feedlot surface becomes anaerobic and starch fermentation in the aged manure begins. Ethanol, acetate, propionate, and butyrate are produced across the entire feedlot pen surface and at much higher concentrations than in the fresh fecal matter, which covers a smaller fraction of the feedlot surface. Some methane may be produced initially from acetate, methanol, and ethanol, but as acids accumulate and the pH drops below 6, methanogenesis stops. A small amount of branched-chain VFA and aromatic compounds are produced by limited protein fermentation. Another consequence of low pH is that more of the VFA becomes protonated and more easily volatilized. As the pen dries out, the fermentation decreases, and the pH rises to its initial value due to the buffering capacity of the soil. If the feedlot remains wet and starch becomes limiting (conditions observed in the aged waste flasks after 3 wk of incubation), it is possible that protein fermentation will become the dominant process producing a wide variety of very malodorous branched-chain VFA and aromatic compounds. Temperature can be factored into the model in two ways, first as a threshold barrier (0°C) for the onset of decomposition and second as the primary regulator of odor production rates (higher temperatures = faster VFA accumulation). Studies measuring the concentrations of potential odor precursors and products in the feedlot soil after such rain events need to be conducted to test this proposed model.

Implications

These studies indicate that malodorous VFA production from manure in feedlot soils is related primarily to starch fermentation rather than to protein or other carbohydrate (i.e., cellulose) fermentation. An immediate application of this finding is to evaluate cattle diets that produce manure with lower starch contents. In theory, manure with lower starch content would produce much less objectionable volatile fatty acid when fermented. Additional insights from this study suggest that soil/manure mixtures enhance volatile fatty acid production by minimizing acidification during manure fermentation. Lowering the soil buffering capacity or inhibiting lactate-consuming microorganisms may decrease odor formation. Field-scale studies need to be conducted to determine the effectiveness of these proposed management strategies on liquid phase, and ultimately gas phase, odor compound concentrations.

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